Indian J. Agric. Res., 53(3) 2019: 255-262
Print ISSN:0367-8245 / Online ISSN:0976-058X

AGRICULTURAL RESEARCH COMMUNICATION CENTRE
www.arccjournals.com

Heterosis studies for yield and agronomic traits in Thai upland rice

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Received: 03-10-2018 Accepted: 16-01-2019 DOI: 10.18805/IJARe.A-390

ABSTRACT

The exploitation of heterosis and heterobeltiosis are the promising way for raising yield potential in crops. Twenty-eight F_1 hybrids and their eight parents were evaluated to estimate the heterosis and heterobeltiosis of yield and other agronomic traits in Thai upland rice. Significant differences of analysis of variance were observed for all studied traits, indicating the existence of worth genetic variability among the hybrids and their parents. The highest significant positive heterosis and heterobeltiosis was attained by Dawk Pa-yawm × Hawm Mali Doi for number of tillers (90.59%; 58.82%) and number of panicles plant^{-1} (60.35%; 46.14%) and panicle length (heterobeltiosis: 20.05%), but highest significant negative heterosis for plant height (-8.90%). Likewise, Nual Hawm × Khun Nan showed the highest significant positive heterosis and heterobeltiosis for yield components, *viz.*, number of filled grains panicle^{-1} (57.39%; 52.25%), spikelet fertility (25.01%; 21.16%), 1000 grain weight (heterosis: 12.85%) and grain yield plant^{-1} (heterosis: 19.86%), but highest significant negative for days to flowering (-17.52%; -6.03%) and days to maturity (-12.00%; -4.91%). These crosses were recommended as the most promising combinations to gain early favorable segregants and developing high yielding upland rice hybrid varieties by heterosis breeding.

Key words: Heterobeltiosis, Heterosis, Hybrid, Upland rice.

INTRODUCTION

Rice (*Oryza sativa* L.) is the paramount staple food crops, but its production tends to decrease due to the shrinking of the potential wetland. It is might be solved by the cultivation of upland rice in the dryland area. However, its productivity stays sluggish around 1 t ha^{-1}. Therefore, hybrid varieties are a current strategy in an attempt to improve upland rice production, by utilizing heterosis or hybrid vigor (Sari *et al.*, 2019). Rice is naturally a self-pollinated crop, but strong heterosis is observed. Heterosis and heterobeltiosis is the phenomenon in which an F_1 hybrid has superior performance over its mid-parent and better parent, respectively (Virmani *et al.*, 1982).

Both negative and positive heterosis are helpful for crop improvement, depending on the breeding targets. Generally, negative heterosis is desirable for early maturity and positive heterosis for high yield (Nuruzzaman *et al.*, 2002). Heterosis breeding is a principal genetic appliance that can facilitate yield enhancement by 30-40% and contributes to raising the desirable qualitative and quantitative traits in cultivated plants (Srivastava, 2000). Various degree of heterosis and heterobeltiosis on cultivars and elite lines of rice were observed by Nevame *et al.* (2012); Sadimantara *et al*. (2014); and Seesang *et al*. (2014) for some agronomic and yield characters. The objectives of this study were to evaluate heterosis and heterobeltiosis of agronomic traits in Thai upland rice for identifying and selecting the favorable parental lines or cross combinations for developing high yielding upland rice varieties.

MATERIALS AND METHODS

The experiment was conducted in which eight Thai upland rice lines *viz.*, Hawm Satun, Dawk Pa-yawm, Dawk Kham, Nual Hawm, Dawk Kha, Hawm Mali Doi, Khun Nan, and Goo Meuang Luang (Table 1) were crossed in half diallel fashion. Hybridization generations (28 F_1) and their 8 parents were planted using a randomized complete block design with two replications at research field Faculty of Natural Resources, Prince of Songkla University, Hat Yai, Songkhla, Thailand (7°00’31’’N, 100°29’46’’E). Each plot comprised of two rows of 4 m length with a space of 30 cm between rows and 25 cm between plants. The NPK (15–15–15) fertilizer was applied at the rate 20 g plant^{-1} before planting and urea (46–0–0) fertilizer was applied following the recommended rate (10 g plant^{-1}) into three splits at 4 and 8 weeks after planting and at panicle initiation stages.

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Table 1: Details of selected Thai upland rice parental lines investigated in the present study.

Selected lines	Source	Type	Yield potency plant^{-1} (g)
Hawm Satun	Farmer, Satun Province, Thailand	White rice	24.17
Dawk Pa-yawm	Rice Research Center, Phatthalung Province, Thailand	White rice	30.44
Dawk Kham	Faculty of Agricultural Technology, King Mongkut's Institute of Technology Ladkrabang, Chumphon Campus, Chumphon Province, Thailand	Red rice	28.51
Nual Hawm	Farmer, Songkhla Province, Thailand	White rice	25.52
Dawk Kha	Rice Research Center, Krabi Province, Thailand	Red rice	29.90
Hawm Mali Doi	Farmer, Chiang Mai Province, Thailand	White rice	26.24
Khun Nan	Farmer, Nan Province, Thailand	White rice	30.28
Goo Meuang Luang	Rice Research Center, Phatthalung Province, Thailand	White rice	28.97

Table 2: Twenty set of rice SSR primers for SSR analysis.

Marker	Chr.	Anneal temp (°C)	PCR Cycles	Min. Allele	Max. Allele
RM 1	1	55	30	67	199
RM 283	1	61	30	130	176
RM 259	1	55	30	133	186
RM 5	1	67	30	94	138
RM 154	2	61	30	148	230
OSR 13	3	53	40	85	122
RM 336	3	55	40	178	184
RM 413	5	53	30	71	114
RM 161	5	61	30	154	187
RM 510	6	57	30	99	127
RM 455	7	57	30	127	144
RM 152	8	53	40	133	157
RM 25	8	53	40	121	159
RM 44	8	53	30	82	132
RM 433	8	53	40	216	248
RM 316	9	55	30	194	216
RM 215	9	55	30	126	161
RM 552	11	55	30	167	258
RM 144	11	57	30	216	295
RM 19	12	55	30	192	250

Source: http://archive.gramene.org/markers/microsat/ssr.html

Ten important agronomic and yield traits were recorded *viz.*, plant height (cm), days to flowering, days to maturity, number of tillers plant^{-1}, number of panicles plant^{-1}, panicle length (cm), number of filled grains panicle^{-1}, spikelet fertility (%), 1000 grain weight (g), and grain yield plant^{-1} (g). Observations were recorded on randomly selected ten plants in both of hybrids and parents for these studied traits. For accuracy of the present study, the true hybrid of F_1 upland rice plants was identified and clarified by simple sequence repeat (SSR) markers by used twenty set of rice SSR primers (Table 2) at Plant Molecular Biotechnology Laboratory, Faculty of Natural Resources, Prince of Songkla University, Hat Yai, Thailand.

The data was subjected to analysis of variance according to Steel and Torrie (1980). The measurement of heterosis and heterobeltiosis commonly is a decrease or increase of the performance of a hybrid in comparison with the mid-parent (average values of two parents) and a better parent that expressed as a percentage (Virmani *et al.*, 1982). The student's t-test based on independent sample method was manifested to determine whether F_1 hybrid means were statistically different over its mid-parent or better parent means according to McDonald (2008). Correlation coefficients were analyzed based on Pearson's correlation coefficients by SPSS program version 16.0 for Windows.

$$\text{Heterosis \%} = \frac{F_1 - MP}{MP} \times 100 \qquad (1)$$

$$\text{Heterobeltiosis \%} = \frac{F_1 - BP}{BP} \times 100 \qquad (2)$$

Equal variances

$$t = \frac{F_1 - \text{MP or BP}}{\sqrt{\frac{(n_1-1)S_1^2 + (n_2-1)S_2^2}{n_1 + n_2 - 2}\left(\frac{1}{n_1} + \frac{1}{n_2}\right)}} \qquad (3)$$

Unequal variance

$$t = \frac{F_1 - MP \text{ or } BP}{\sqrt{\frac{S_1^2}{n_1} + \frac{S_2^2}{n_2}}} \qquad (4)$$

Where, F_1 = F_1 hybrid value, MP = mid-parent value, BP = better parent value, S_1^2 = variance of group 1 (maximum value), S_2^2 = variance of group 2 (minimum value), n_1 = number of samples in group 1, n_2 = number of samples in group 2, group = F_1 hybrid, MP or BP.

RESULTS AND DISCUSSION

The authenticity of F_1 upland rice hybrids: Twenty set of rice SSR primers were surveyed on the eight parents to identify the segregation pattern among them. Out of these, six set of rice SSR primers *viz.*, RM 1, RM 5, RM 44, RM 144, RM 215 and RM 510 produced single band marker which clearly distinguished the parents. Specific SSR primers to verify the hybrid authenticity of F_1 upland rice plants for each cross combination in the present study are presented in Table 3.

Analysis of variance: The genotypic difference among Thai upland rice genotypes was confirmed by analysis of variance of the recorded data on different indicated traits (Table 4). The results showed that there were highly significant differences among genotypes, among parents, and among hybrids in all studied traits. The difference among parents indicated that each of them had different characters and they were appropriate for genetic and hybrid studies. The genotypic differences among hybrids indicated that they were eligible to further analysis *i.e.*, the estimation of heterosis and heterobeltiosis, because different hybrid will show different characters. The significant differences of parents vs. hybrids in all studied traits (except for plant height, number of filled grains panicle^{-1} and 1000 grain weight), indicated that the pair of parents and hybrids will expose different characters which had significant heterosis and heterobeltiosis. The coefficient of variation (CV) was less than 17% for each trait indicating the accuracy of data obtained.

Mean performance: Mean values of parents and their hybrids are given in Table 5. There was a high variation of data that confirmed worth genetic variability in both of parents and hybrids group, indicated that different genetic systems were involved in controlling traits, and also emphasized the important study of these traits.

Heterosis (H) and heterobeltiosis (Hb): The degree of H and Hb in this study was varied among crosses and traits (Table 6), which in accordance with Alam *et al.* (2004) and Singh *et al.* (2011) who observed the varying degree of heterosis and heterobeltiosis for yield and its attributes in upland rice hybrids.

Negative direction of H and Hb was desired for plant height, DP × HMD showed the highest significant negative heterosis (-8.90%), followed by DP × KN (-8.62%). Meanwhile, significant negative heterobeltiosis was observed only in the hybrid KN × GML (-7.15%). Thus, these hybrids can be used to generate semi-dwarf varieties in the next breeding programs. Negative heterosis for rice plant height in several crosses was notified by Nuruzzaman *et al.* (2002) and Alam *et al.* (2004). The partial harvesting of lodged plants and increasing of diseases and pests can reduce the

Table 3: Specific SSR primers for each cross combination of F_1 upland rice hybrid.

Primers	Cross combinations
RM 1	DP × GML, DM × KN, DM × GML, NH × GML, DK × KN, DK × GML, HMD × GML, KN × GML
RM 5	HS × DM, HS × DK, HS × HMD, HS × KN, HS × GML, DP × DM, DP × DK, DP × HMD, DP × KN, DM × NH, NH × DK, NH × HMD, NH × KN, DK × HMD
RM 44	HS × DP, DM × DK, DM × HMD
RM 144	HMD × KN
RM 215	HS × NH
RM 510	DP × NH

Table 4: Analysis of variance for studied traits in Thai upland rice genotypes.

Source	df	Mean square of traits									
		PH	DF	DM	NT	NP	PL	NFG	SF	1000-GW	GYP
Genotypes	35	**	**	**	**	**	**	**	**	**	**
Parents vs. Hybrids	1	ns	**	*	**	*	**	ns	**	ns	*
Among Parents	7	**	**	**	**	**	**	**	**	**	**
Among Hybrids	27	**	**	**	**	**	**	**	**	**	**
CV (%)		6.22	2.72	1.64	16.35	15.92	3.67	11.36	5.88	4.78	5.25

PH = plant height; DF = days to flowering; DM = days to maturity; NT = number of tillers plant^{-1}; NP = number of panicles plant^{-1}; PL = panicle length; NFG = number of filled grains panicle^{-1}; SF = spikelet fertility; 1000-GW = 1000 grain weight; GYP = grain yield plant^{-1}; CV = coefficient of variation; ** = significant at 1%; * = significant at 5%; ns = non-significant.

quantity and quality of grains. Hence, breeders prefer the plants with stiff culms and short height, besides semi-dwarf plants are high yielder due to increased tillering ability, resistance to lodging and better responsiveness to nitrogen fertilizer (Saleem *et al.*, 2008). Rahimi *et al.* (2010) also reported the presence of the significant negative correlation between plant height and rice grain yield. So, obtaining semi-dwarf plants was one of the important factors in the rice breeding program.

Development of high yielding early maturing varieties is the main target in rice breeding programs. Regarding the characters days to flowering and days to maturity, significant negative heterosis was observed in seven and nine crosses, respectively. Among 28 crosses, the highest significant negative heterosis (-17.52%; -12.00%) and heterobeltiosis (-6.03%; -4.91%) was observed in NH × KN for both of these traits, indicated an over-dominance type of gene action was considered for it, while DP × HMD exhibited significant negative value (-11.63%; -7.04%) only over its mid-parent indicating partial dominant type of gene action. Thus, these cross combinations were suggested as a chance for developing early maturity varieties. Negative heterosis for earliness of flowering and maturity in hybrid rice was also observed by Aananthi and Jebaraj (2006).

Table 5: Mean performance of eight parents and 28 F_1 Thai upland rice hybrids for the studied traits.

	Means of traits									
Genotypes	**PH (cm)**	**DF (day)**	**DM (day)**	**NT (no)**	**NP (no)**	**PL (cm)**	**NFG (no)**	**SF (%)**	**1000-GW (no)**	**GYP (g plant^{-1})**
Hawm Satun (HS)	107.08	120.00	152.85	8.50	8.50	24.93	185.32	60.73	19.11	24.17
Dawk Pa-yawm (DP)	104.13	105.15	141.15	20.40	15.80	28.38	**217.90**	**80.35**	24.22	**30.44**
Dawk Kham (DM)	108.44	114.20	149.25	**39.10**	21.80	**31.17**	179.10	79.35	25.62	28.51
Nual Hawm (NH)	109.63	99.75	134.80	35.30	**24.50**	23.54	115.43	66.87	24.53	25.52
Dawk Kha (DK)	102.28	104.00	140.10	35.70	22.30	27.29	105.87	68.84	25.12	29.90
Hawm Mali Doi (HMD)	**98.77**	**72.05**	**110.15**	13.60	13.00	27.55	99.43	78.01	30.58	26.24
Khun Nan (KN)	145.40	78.00	116.10	36.40	10.80	30.66	123.50	71.26	32.81	30.28
Goo Meuang Luang (GML)	145.53	103.95	142.05	22.40	15.00	30.67	123.70	71.85	**33.72**	28.97
HS × DP	120.34	112.07	146.10	14.23	11.87	27.63	191.43	71.71	23.71	29.58
HS × DM	110.63	109.69	148.00	20.00	12.50	31.69	193.57	73.43	22.03	26.05
HS × NH	110.01	111.20	144.80	23.50	17.50	24.23	140.04	63.46	22.67	25.59
HS × DK	116.80	115.31	148.45	18.10	12.30	27.08	158.46	69.89	23.22	28.88
HS × HMD	99.95	94.38	126.33	15.00	12.33	28.74	165.19	70.84	24.67	26.58
HS × KN	124.93	96.05	127.18	33.95	13.91	30.87	173.24	67.67	28.39	30.41
HS × GML	141.67	109.25	145.75	28.00	15.25	28.27	96.53	44.32	25.58	24.94
DP × DM	110.37	114.48	148.10	31.90	19.80	29.32	185.01	73.28	24.38	30.98
DP × NH	109.50	107.49	143.45	26.55	19.09	29.15	182.54	64.74	22.84	28.37
DP × DK	112.16	115.86	149.95	30.10	19.86	30.41	181.87	76.74	25.17	31.57
DP × HMD	**92.42**	78.30	116.80	32.40	23.09	34.07	**225.34**	**88.93**	30.18	32.94
DP × KN	114.00	100.31	138.45	35.40	14.80	27.97	146.58	73.92	27.07	29.99
DP × GML	135.23	117.29	151.86	23.57	17.87	26.97	148.06	55.83	26.36	28.81
DM × NH	113.49	110.55	143.85	33.67	17.33	25.27	121.10	67.70	25.34	27.22
DM × DK	107.35	110.51	143.05	35.67	20.67	26.18	119.74	65.57	26.17	28.53
DM × HMD	108.87	84.26	121.80	40.75	23.83	32.84	151.13	70.54	30.02	30.03
DM × KN	120.08	93.35	124.30	50.71	20.70	31.82	158.82	68.64	30.55	32.29
DM × GML	142.31	115.95	149.50	36.29	20.86	29.01	128.56	65.20	28.36	26.81
NH × DK	118.60	113.59	149.05	49.70	**30.30**	28.44	150.10	74.77	25.69	30.30
NH × HMD	113.27	81.75	117.50	40.33	23.50	30.95	151.28	80.21	30.60	30.66
NH × KN	118.24	**73.30**	**110.40**	**51.70**	25.02	**35.83**	188.03	86.34	**32.35**	**33.43**
NH × GML	142.20	107.50	142.50	39.00	26.06	30.79	120.94	65.78	28.10	27.76
DK × HMD	98.50	96.49	135.40	28.64	19.80	32.03	106.70	66.04	28.94	29.96
DK × KN	122.02	99.24	136.50	30.00	13.00	29.38	93.77	68.71	27.46	29.67
DK × GML	143.92	114.25	151.25	23.75	14.85	29.43	100.63	42.67	26.95	29.06
HMD × KN	117.08	88.92	117.71	31.51	14.50	27.71	84.06	50.56	23.92	26.02
HMD × GML	113.00	91.88	127.25	17.00	13.00	32.40	98.24	46.08	27.70	25.78
KN × GML	135.00	99.00	137.50	34.20	14.50	31.50	95.20	45.80	23.38	28.71
$LSD_{0.01}$	19.92	7.54	6.11	13.45	7.70	2.93	44.75	10.84	3.46	4.11

PH = plant height; DF = days to flowering; DM = days to maturity; NT = number of tillers plant^{-1}; NP = number of panicles plant^{-1}; PL = panicle length; NFG = number of filled grains panicle^{-1}; SF = spikelet fertility; 1000-GW = 1000 grain weight; GYP = grain yield plant^{-1}; **Bold** indicates the highest value for each trait in desirable direction.

Table 6: Heterosis (H) and heterobeltiosis (Hb) in percentage for the studied traits in F_1 Thai upland rice hybrids.

	Heterosis and heterobeltiosis (%) of traits																			
	PH		DF		DM		NT		NP		PL		NFG		SF		1000-GW		GYP	
Hybrids	**H**	**Hb**	**H**	**Hb**	**H**	**Hb**	**H**	**Hb**	**H**	**Hb**	**H**	**Hb**	**H**	**Hb**	**H**	**Hb**	**H**	**Hb**	**H**	**Hb**
HS × DP	13.95**	15.57**	-0.45	6.58**	-0.61	3.51**	-1.52	-30.25*	-2.35	-24.91	3.66	-2.64	-5.05	-12.15*	1.66	-10.75**	9.46**	-2.10	8.33*	-2.83
HS × DM	2.66	3.31	-6.33**	-3.95**	-2.02**	-0.84	-15.97	-48.85**	-17.49	-42.66**	12.98*	1.67	6.23	4.45	4.85	-7.45	-1.46	-13.99**	-1.12	-8.66**
HS × NH	1.52	2.73	1.20	11.47**	0.68	7.42**	7.31	-33.43**	6.06	-28.57**	-0.03	-2.82	-6.88	-24.44**	-0.53	-5.10	3.93	-7.56**	3.01	0.29
HS × DK	11.58**	14.20**	2.96**	10.88**	1.35	5.96**	-18.10*	-49.30**	-20.13**	-44.84**	3.73	-0.75	8.83	-14.50	7.87	1.52	5.02	-7.56**	6.83*	-3.41
HS × HMD	-2.89	1.20	-1.71	31.00**	-3.93**	14.69**	35.75	10.29	14.70	-5.15	9.53**	4.33	16.03	-10.86	2.12	-9.18	-0.69	-19.33**	5.46	1.30
HS × KN	-1.04	16.66**	-2.98**	23.14**	-5.43**	9.54**	51.22**	-6.73	44.09	28.75	11.06**	0.69	12.20*	-6.52	2.54	-5.03	9.37**	-13.47**	11.72**	0.45
HS × GML	12.17**	32.30**	-2.43	5.10**	-1.15*	2.60**	81.23**	25.00**	29.79**	1.67	1.68	-7.84*	-37.53**	-47.92**	-33.14**	-38.32**	-3.15	-24.14**	-6.11	-13.89
DP × DM	3.84	5.99	4.38**	8.87**	2.00*	4.92**	7.23	-18.41*	5.32	-9.17	-1.53	-5.93**	-6.80	-15.09**	-8.23**	-8.80**	-2.17	-4.83	5.10*	1.77
DP × NH	2.46	5.16	4.91*	7.75**	3.97**	6.42**	-4.67	-24.79**	-5.29	-22.10**	12.30**	2.72	9.53**	-16.23**	-12.05*	-19.42**	-6.28**	-6.87**	1.41	-6.79**
DP × DK	8.68**	9.66**	10.79**	11.40**	6.63**	7.03**	7.31	-15.69	4.27	-10.93	9.26**	7.17**	12.35*	-16.53**	2.88	-4.49	2.01	0.18	4.63*	3.70
DP × HMD	**-8.90****	-6.43	-11.63**	8.67**	-7.04**	6.04**	**90.59****	**58.82****	**60.35****	**46.14****	21.83**	**20.05****	42.02**	3.41	12.32**	10.68**	10.14**	-1.32	16.24**	8.22**
DP × KN	-8.62**	9.48*	9.53**	28.60**	7.64**	19.25**	24.65	-2.75	11.28	-6.33	-5.25*	-8.77**	-14.13**	-32.73**	-2.48	-8.00**	-5.07**	-17.49**	-1.23	-1.49
DP × GML	8.33**	29.87**	12.18**	12.83**	7.25**	7.59**	10.14	5.22	16.01	13.07	-8.64**	-12.05**	-13.32*	-32.05**	-26.63**	-30.51**	-9.01**	-21.83**	-3.01	-5.36*
DM × NH	4.08	4.65	3.34*	10.83**	1.28	6.71**	-9.50	-13.90	-25.16**	-29.29**	-7.64**	-18.94**	-17.77**	-32.39**	-7.40	-14.68**	1.06	-1.08	0.78	-4.52
DM × DK	1.88	4.95	1.29	6.26**	-1.12	2.11*	-4.64	-8.79	-6.26	-7.31	-10.43**	-16.01**	-15.96	-33.14**	-11.50*	-17.36**	3.18	2.18	-2.30	-4.56*
DM × HMD	5.08	10.23*	-9.52**	16.95**	-6.09**	10.58**	54.65**	4.22	36.93**	9.29	11.84**	5.34*	8.52	-15.62**	-10.34**	-11.10**	6.84**	-1.84	9.70**	5.32*
DM × KN	-5.39*	10.73**	-2.86*	19.68**	-6.31**	7.06**	34.33**	29.69**	26.99**	-5.05	2.94	2.09	4.97	-11.32*	-8.85*	-13.50**	4.57**	-6.89**	9.85	6.65
DM × GML	12.07**	31.23**	6.30**	11.54**	2.64*	5.24**	18.00	-7.20	13.34	-4.33	-6.17**	-6.92**	-15.09**	-28.22**	-13.75**	-17.82**	-4.42*	-15.90**	-6.71**	-7.44**
NH × DK	11.94**	15.96**	11.49**	13.87**	8.44**	10.57**	40.00**	39.22**	29.49**	23.67**	11.90**	4.21	35.65**	30.03**	10.19*	8.61	3.48*	2.26	9.36	1.35
NH × HMD	8.71	14.69*	-4.83**	13.46**	-4.06**	6.67**	64.95**	14.25	25.33**	-4.08	21.17**	12.36**	40.82**	31.06**	10.73**	2.83	11.07**	0.08	18.50**	**16.87****
NH × KN	-7.27**	7.85*	**-17.52****	**-6.03****	**-12.00****	**-4.91****	44.21**	42.03**	41.76**	2.12	**32.21****	16.86**	**57.39****	**52.25****	**25.01****	**21.16****	**12.85****	-1.38	**19.86****	10.43**
NH × GML	11.46	29.71*	5.55*	7.77**	2.94*	5.71**	35.18**	10.48	31.95**	6.37	13.59**	0.39	1.15	-2.23	-5.17	-8.46*	-3.51	-16.66*	1.91	-4.16
DK × HMD	-2.01	-0.26	9.62**	33.93**	8.21**	22.92**	16.19	-19.78*	12.18	-11.21	16.81**	16.26**	3.94	0.78	-10.06**	-15.34**	3.90*	-5.37**	6.74**	0.22
DK × KN	-1.47	19.30**	9.05**	27.23**	6.56**	17.57**	-16.78*	-17.58*	-21.45*	-41.70**	1.39	-4.18	-18.23*	-24.07**	-1.92	-3.58	-5.18**	-16.28**	-1.37	-1.99
DK × GML	16.15**	40.71**	9.88**	9.91**	7.21**	7.96**	-18.24	-33.47**	-20.38*	-33.41**	1.55	-4.05	-12.33*	-18.65**	-39.34**	-40.61	-8.39**	-20.07	-1.25	-2.79
HMD × KN	-4.10	18.54*	18.52**	23.41**	4.05**	6.86**	26.03**	-13.44	21.85	11.54	-4.80	-9.62**	-24.58*	-31.93**	-32.26**	-35.19	-24.52**	-27.08	-7.91**	-14.05**
HMD×GML	-7.49*	14.41*	4.40**	27.52**	0.91	15.52**	-5.56	-24.11*	-7.14	-13.33	11.31*	5.64	-11.95	-20.59*	-38.50**	-40.92	-13.83**	-17.85	-6.60	-11.00**
KN × GML	-7.19**	**-7.15****	8.82**	26.92**	6.53**	18.43**	16.33*	-6.04	12.40	-3.33	2.72	2.71	-22.98**	-23.04**	-36.00**	-36.26	-29.72**	-30.67	-3.07	-5.17

PH = plant height; DF = days to flowering; DM = days to maturity; NT = number of tillers plant^{-1}; NP = number of panicles plant^{-1}; PL = panicle length; NFG = number of filled grains panicle^{-1}; SF = spikelet fertility; 1000-GW = 1000 grain weight; GYP = grain yield plant^{-1}; ** = significant at 1%; * = significant at 5%; **Bold** indicates the highest significant value for each trait in desirable direction.

Table 7: Correlation coefficients of heterosis (H) and heterobeltiosis (Hb) for the studied traits.

Traits		**Correlation coefficients**								
		DF	**DM**	**NT**	**NP**	**PL**	**NFG**	**SF**	**1000-GW**	**GY**
PH	H	0.19	0.27	-0.16	-0.24	-0.20	-0.12	-0.06	0.17	-0.09
	Hb	-0.15	-0.19	-0.05	-0.03	-0.37	-0.21	-0.36	-0.35	-0.32
DF	H		0.92^{**}	-0.46^{*}	-0.40^{*}	-0.59^{**}	-0.57^{**}	-0.53^{**}	-0.66^{**}	-0.65^{**}
	Hb		0.93^{**}	-0.06	0.10	0.04	-0.27	-0.29	-0.37	-0.06
DM	H			-0.50^{**}	-0.47^{*}	-0.48^{*}	-0.50^{**}	-0.44^{*}	-0.57^{**}	-0.59^{**}
	Hb			-0.11	0.001	0.10	-0.23	-0.25	-0.31	-0.05
NT	H				0.92^{**}	0.45^{*}	0.41^{*}	0.22	0.31	0.47^{*}
	Hb				0.78^{**}	0.37	0.40^{*}	0.34	0.17	0.47^{*}
NP	H					0.47^{*}	0.48^{*}	0.25	0.28	0.50^{**}
	Hb					0.29	0.22	0.14	0.03	0.25
PL	H						0.83^{**}	0.52^{**}	0.45^{*}	0.72^{**}
	Hb						0.74^{**}	0.47^{*}	0.30	0.60^{**}
NFG	H							0.77^{**}	0.65^{**}	0.88^{**}
	Hb							0.71^{**}	0.49^{**}	0.68^{**}
SF	H								0.79^{**}	0.77^{**}
	Hb								0.69^{**}	0.72^{**}
1000-GW	H									0.79^{**}
	Hb									0.63^{**}

PH = plant height; DF = days to flowering; DM = days to maturity; NT = number of tillers plant^{-1}; NP = number of panicles plant^{-1}; PL = panicle length; NFG = number of filled grains panicle^{-1}; SF = spikelet fertility; 1000-GW = 1000 grain weight; GYP = grain yield plant^{-1}; ** = significant at 1%; * = significant at 5%.

The magnitude of hybrid vigor was highest for number of tillers plant^{-1}. The heterosis and heterobeltiosis values ranged from -18.24 to 90.59% and -49.30 to 58.82%, respectively (Table 6). The highest significant positive heterosis (90.59%) and heterobeltiosis (58.82%) being in DP × HMD due to over-dominant type of gene action. However, Virmani *et al*. (1982) reported increasing of grain yield was not fully affected by highly positive heterosis for tillers number due to an increased number of spikelets per unit area indicated that some tillers were not the productive tillers. It was occurred in this research, the hybrid DP × HMD had the highest heterosis and heterobeltiosis value for number of tillers plant^{-1} but had not the highest value for other yield attributes, such as number of filled grains panicle^{-1} and spikelet fertility. The present findings are similar to earlier reports of Bagheri and Jelodar (2010) who reported a hybrid had maximum significant positive heterosis and heterobeltiosis for number of tillers plant^{-1} but had not the highest value for other yield traits, such as panicle length and number of spikelets panicle^{-1}.

With regard to number of panicles plant^{-1}, positive heterosis is desirable. DP × HMD had the highest significant positive heterosis (60.35%) and heterobeltiosis (46.14%). Generally, an increasing number of productive tillers plant^{-1} followed by increasing of number of panicles plant^{-1} (number of tillers greater than number of panicles), but this is not ensure the highest grain yield because depend on others yield-related traits, like panicle length, number of filled grains panicle^{-1}, spikelet fertility, etc. The observation of heterosis and heterobeltiosis for number of tillers and number of panicles plant^{-1} traits by Rashid *et al*. (2007) and Rahimi *et al*. (2010) were also similar, that most of the investigated crosses had the significant positive value which number of tillers value was greater than number of panicles plant^{-1}.

In rice, long panicle with more of filled grains provides an opportunity for more yields, so positive heterosis is desirable for panicle length character. Out of 28 crosses, the significant positive values were observed in 13 crosses over mid-parent and six crosses over better parent with the maximum value being attained by NH × KN (32.21%) for heterosis and DP × HMD (20.05%) for heterobeltiosis, indicating partial dominant type of gene action for both of these hybrids. Conformable result was reported by Nevame *et al*. (2012) and Patil *et al*. (2012) that positive heterobeltiosis was identified for panicle length indicates the genes from the parents that controlling its related traits interacted favorably and resulted in positive grain yield heterosis in most hybrids.

The hybrid NH × KN had maximum significant positive heterosis and heterobeltiosis for number of filled grains panicle^{-1} (57.39% and 52.25%) and spikelet fertility (25.01% and 21.16%). Shanthi *et al*. (2006) and Sadimantara *et al*. (2014) reported that several crosses had significant positive value for these traits. However, these results are in contrary with Joshi (2001) who reported that positive significant standard heterosis and heterobeltiosis were absence for spikelet fertility percentage in some crosses. It was supposedly because the pollen parents of these sterile hybrids might not have restorer genes.

The maximum significant positive heterosis of 1000 grain weight being observed in NH × KN (12.85%) but for heterobeltiosis there were not significant positive value in all crosses, it was alleged because of the ANOVA results in a source of variation parents vs. hybrids was not significant difference for this trait. Moreover, the highest significant positive heterosis of grain yield plant^{-1} being attained by NH × KN (19.86%), while for heterobeltiosis was in NH × HMD (16.87%). The grain yield has become the main goal in the breeding program as it is interrelated to other traits, so those hybrids of each trait that related to grain yield as discussed previously were identified as the most promising combinations for developing high yielding upland rice varieties. Out of 28 crosses investigated in the present study, six expressed superiority for grain yield over mid-parent and three crosses over better parent (highly significant differences), indicating non-additive gene action plays a role, as was also reported by Reddy *et al*. (2012). A high percentage of heterosis for grain yield and its components in upland rice was revealed by Alzona and Arrauadeau (1995); and Singh *et al*. (2011).

Two principal hypotheses have been proposed to explain the genetic basis of heterosis, *i.e*., dominance hypothesis: heterosis is due to the accumulation of favorable dominant genes in a hybrid derived from two parents (Davenport, 1908) and over-dominance hypothesis: heterozygote (Aa) is more vigorous and productive than either homozygotes (AA or aa) (East, 1936). Epistasis might be a key genetic basis of heterosis in rice as suggested by Li *et al*. (1997). Earlier studies have shown that heterosis is the result of partial to complete dominance, over-dominance, epistasis, and it might be a combination of all these (Comstock and Robinson, 1952). Bagheri and Jelodar (2010) inferred that over-dominant type of gene action indicated if highly significant in both types of heterosis and higher mean performance, partial dominant type of gene action manifested if significant mid-parent heterosis but non-significant in heterobeltiosis, and if non-significant in both of it representing an additive type of gene action. These results are in conformity with earlier findings by Shanthi *et al*. (2006) and Rashid *et al*. (2007) in diverse rice varieties from different origin.

Furthermore, according to Falconer and Mackay (1996), heterosis directly depends on the presence of dominance gene action and its magnitude relies on a magnitude of directional dominance, and indirectly on the interaction implicating dominance effect at different loci and its magnitude depends on the different level of the gene frequency of two parents at all the loci affecting the related trait. Whereas, the gene frequency different derived from the diverse genetic background of the parental lines. Manjarrez *et al*. (1997) stated that the wide genetic distance between parents will be expanding the gene differences and great potential interaction of genes in the form of dominance and epistasis thus enlarging the potential of heterosis.

Relationships among heterosis and heterobeltiosis of the studied traits: The heterosis of grain yield plant^{-1} was negatively significant correlated with days to flowering and maturity, whereas there was a highly significant positive correlation of hybrid vigor (heterosis and heterobeltiosis) in most of the studied traits (Table 7). Therefore, the characters number of filled grains panicle^{-1}, spikelet fertility, and 1000 grain weight were considered major contributors to grain yield of upland rice hybrids in this study, since they showed the highly significant positive correlation in both of heterosis and heterobeltiosis on single plant yield trait. The results were in accordance with the findings by Toshimenla *et al*. (2016) who concluded that exploitation of heterosis in upland rice is determined by grain yield plant^{-1} which is contributed by filled grains and grain weight.

CONCLUSION

In an ideal situation, upland rice hybrids with semi-dwarf plant type, earliness flowering and maturity, high productive tillers and panicles number, high grain yield and its contributing traits are preferable. Keeping in view of mean performance, heterosis and heterobeltiosis value, and the correlations of them, two most promising crosses *viz*., Dawk Pa-yawm × Hawm Mali Doi and Nual Hawm × Khun Nan can be considered as the Thai upland rice F_1 hybrids to gain early favorable segregants and developing high yielding upland rice hybrid varieties. It also indicates that some traits, such as number of filled grains panicle^{-1}, spikelet fertility, and 1000 grain weight were highly positive correlation with grain yield and essential to the efficiency of upland rice breeding programs.

ACKNOWLEDGMENT

This research was supported by the Higher Education Research Promotion and The Thailand's Education Hub for Southern Region of ASEAN Countries Project Office of the Higher Education Commission. This work was supported by the government budget of Prince of Songkla University (NRT550033S and NAT582077S). It was partially supported by the Center of Excellence in Agricultural and Natural Resources Biotechnology (CoE-ANRB): phase 2, Faculty of Natural Resources and the Graduate School, Prince of Songkla University.

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